Transactions of the American Fisheries Society 136:706–717, 2007

DOI: 10.1577/T06-275.1

[Article]

Regional Synchrony of Brown Trout and Brook Trout Population Dynamics among Michigan Rivers

TROY G. ZORN*

Michigan Department of Natural Resources, Marquette Fisheries Research Station, 484 Cherry Creek Road, Marquette, Michigan 49855, USA

ANDREW J. NUHFER

Michigan Department of Natural Resources, Hunt Creek Fisheries Research Station, 1581 Halberg Road, Lewiston, Michigan 49756, USA

Abstract.—The ability to describe regional patterns in trout density would be useful for biologists concerned with population status across large regions as well as managers of rivers at the local scale. Noting the importance of flow conditions at the time of emergence to trout year-class strength in Michigan streams and the influence of age-0 trout abundance on subsequent abundance of older age-classes, we assessed the potential for regional synchrony in the population dynamics of brown trout *Salmo trutta* and brook trout *Salvelinus fontinalis* among Michigan rivers. We used correlation analyses to look for regional synchrony in May stream discharge (approximating the time of brown trout fry emergence) and fall trout density among many Michigan trout streams. We found a high degree of synchrony in average May discharge among streams, particularly those in the northern portion of Michigan's Lower Peninsula. There were significant correlations in the long-term densities of brown trout and brook trout year-classes among several rivers in this area, including sites up to 140 km apart and rivers draining into different Great Lakes. Predicted numbers of days to 50% swim-up of brown trout fry were similar among four streams and synchronous, further supporting the hypothesis of synchrony in trout population dynamics in Michigan streams at the regional scale. Long-term trout population estimates and streamflow data collected from a network of long-term index (fixed) sites throughout Michigan will aid in further description of the spatial extent of synchrony in trout populations.

Stream fisheries for brown trout *Salmo trutta* and brook trout *Salvelinus fontinalis* represent an important but dispersed resource in Michigan. With nearly 8,000 km (5,000 mi) of trout streams spread across the state, managers with limited field sampling resources are charged with the daunting tasks of assessing trends in trout populations, determining the need for local management actions, and assessing effectiveness of past management activities. Complicating management's assessment of their actions is the substantial, seemingly stochastic variation in trout population levels that occurs naturally. An ability to describe regional patterns in trout density would be useful for biologists describing population status across large regions as well as managers of rivers at the local scale.

The regional-scale influences of climate on streamflow and its subsequent effect on age-0 trout imply that trout population dynamics may be synchronous among streams within a region (Zorn and Nuhfer 2007, this issue). High flow conditions during incubation and at the time of fry emergence have been negatively correlated with year-class strength and subsequent density of older age-classes of stream dwelling brown trout (Strange et al. 1992; Nuhfer et al. 1994; Jensen and Johnsen 1999; Spina 2001; Cattanéo et al. 2002; Lobón-Cerviá 2004). Negative effects of high flows on year-class strength have been documented in one Michigan trout stream (Nuhfer et al. 1994), but the hydrologic stability and low-gradient (low-power) nature of most Michigan trout streams may prevent widespread occurrence of flow-induced variation in trout populations. Climate in Midwestern states such as Michigan is a regional phenomenon, so that year-to-year variation may be similar across much of the state. Thus, the occurrence of synchrony in trout population dynamics among Midwestern streams seems possible.

The objective of this study was to explore the potential for regional synchrony in brown trout and brook trout populations among Michigan rivers. We approached the objective from a couple of perspectives. First, we examined correlations in long-term data on spring stream discharge and fall trout density among many rivers to look for shared temporal patterns at the regional scale (i.e., regional synchrony). Second, we compared estimated swim-up times of brown trout fry

* Corresponding author: zornt@michigan.gov

Received December 15, 2006; accepted December 23, 2006
Published online May 3, 2007

TABLE 1.—Data period and number of years of fish survey data, physical dimensions, mean July water temperature, discharge, and slope for long-term trout population index stations in northern Michigan. Mean July temperatures were derived from hourly measurements by electronic thermometers. Flow stability values, expressed as the ratio of the 10% and 90% exceedance flows, occur for rivers where U.S. Geological Survey gauging station data were available. Slope values were calculated using the 1:100,000-scale National Hydrologic Database and represent the channel's vertical drop divided by its length for the confluence-to-confluence segment containing the population index station. For some stations, data were not available for all years of the data period.

Station	Data period (years of data)	Station length (m)	Station width (m)	Mean July temperature (°C)	Summer discharge (m^3/s)	Flow stability	Slope
Main-stem Au Sable River							
Gauge at Grayling					2.15	1.92	
Thendara Road	1960–2001 (31)	236	29	16.8	6.06		0.0013
North Branch Au Sable River							
Eamon's Landing	1962–2001 (33)	305	33				0.0016
South Branch Au Sable River							
Smith Bridge (State Route 72)	1974–2003 (26)	274	22	16.6	3.99	3.11	0.0017
Manistee River							
Gauge near State Route 72					5.10	1.34	
Cameron Bridge Road	1988–2003 (16)	418	14	12.4			0.0005
Pere Marquette River							
Upstream from the Baldwin River	1981–2003 (20)	319	17	16.4	2.97		0.0016
South Branch Paint River							
Upper Goldmine Road	1990–2004 (15)	305	15		1.54		0.0013
Hunt Creek							
Below z-weir	1995–2004 (9)	700	7	16.0	0.71		0.0035
Gilchrist Creek							
Upstream from County Road 612	1995–2004 (10)	2,300	8	16.1	1.10		0.0021

in four rivers to determine if they were similar and synchronous among years.

Methods

Study area.—We used data from coldwater streams scattered throughout Michigan (Tables 1, 2; Figures 1, 2). All streams have relatively stable, groundwater-dominated flows due to the combination of coarse-textured geology and topographic slope in their catchments (Wiley et al. 1997). Populations of brown trout and brook trout in these streams are sustained entirely by natural reproduction.

Correlation analyses.—We assessed synchrony in flow conditions and trout dynamics among rivers by means of correlation analyses. We used long-term data on age-class density from the South Branch Paint River in Michigan's Upper Peninsula and several sites in the northern half of Michigan's Lower Peninsula, namely, the Au Sable River system, Manistee and Pere Marquette rivers, and Hunt and Gilchrist creeks (Table 1; Figure 1). Brown trout were present in all streams with fish data, and sympatric with brook trout in the Manistee River, Hunt Creek, and three branches of the Au Sable River.

Trout populations at all sites were assessed in fall (usually September) by two-pass mark–recapture electrofishing with either a two- or three-anode, 240-V DC tow barge electrofishing unit. Two anodes were used on Hunt and Gilchrist creeks, while three anodes were used on the other larger streams. We computed population estimates by 25-mm length-groups of trout using the Chapman modification of the Petersen mark–recapture method (Ricker 1975). Every year, we aged 10 or more trout per 25-mm length-group (if sufficient fish were available) from scales (dorsal fin rays on the South Branch Paint River) and used the aging results to apportion population estimates by length-groups into estimates by age-group. We used Pearson correlations to compare fall densities of age-0 to age-2 brown trout and age-0 to age-1 brook trout among rivers. Since the sample sizes for some sites were relatively small, we considered correlations significant at P-values of 0.10 or less.

We assessed the year-to-year similarity in streamflow conditions in spring (near the time of brown trout fry emergence) for a broader array of trout streams. Included were some rivers where U.S. Geological Survey (USGS) gauges were located in downstream reaches having summer temperatures too warm for trout (Table 2; Figure 2). Average May stream discharge data were downloaded from the USGS website for each site for the period of record. We used data for May because we thought it would simultaneously characterize trout emergence and spring runoff periods across the entire state better than any other single month. We assessed hydrologic synchrony

TABLE 2.—Attributes of coldwater rivers with U.S. Geological Survey streamflow gauges and years for which mean May discharge data were available. Site numbers correspond to the locations shown in Figure 4.

Site	Location	Gauge number	Period of record	Catchment area (km^2)
1	Cherry Creek near Harvey	4044583	1966–1970, 1980–1981	12
2	Iron River at County Highway 424 at Caspian	4060500	1948–1980	239
3	Paint River near Alpha	4062000	1953–2004	1,634
4	Augusta Creek near Augusta	4105700	1965–2004	101
5	Pere Marquette River at Scottville	4122500	1940–2004	1,764
6	Manistee River near Grayling	4123500	1934–1973	319
7	Pine River near Hoxeyville	4125500	1953–1982	650
8	Little Manistee River near Freesoil	4126200	1957–1975	461
9	Platte River at Honor	4126740	1990–2004	306
10	Boardman River near Mayfield	4127000	1953–1989	471
11	Jordan River near East Jordan	4127800	1967–2004	176
12	Sturgeon River at Wolverine	4127997	1942–2004	497
13	Pigeon River at Sturgeon Valley Road near Vanderbilt	4128990	1951–2004	149
14	Black River near Tower	4130500	1943–2000	805
15	Main-stem Au Sable River at Grayling	4135500	1943–1993	285
16	East Branch Au Sable River at Grayling	4135600	1958–1984	197
17	South Branch Au Sable River near Luzerne	4135700	1967–1989, 1991–2004	1,039
18	Rifle River at State Road at Selkirk	4140500	1951–1982	303
19	Paint Creek at Rochester	4161540	1960–2004	184

between sites by computing Pearson correlations for years when average May discharge data were available for both sites. We considered correlations significant at P-values of 0.05 or less.

Swim-up dates of fry in rivers.—We used redd count observations, winter stream temperature data, and an existing model (Crisp 1988) to predict the number of days to 50% swim-up of brown trout fry in Gilchrist Creek, Hunt Creek, and the main-stem and South Branch Au Sable River. Crisp's (1988) model predicts the number of days from egg fertilization to 50% swim-up of fry based upon incubation temperatures. The

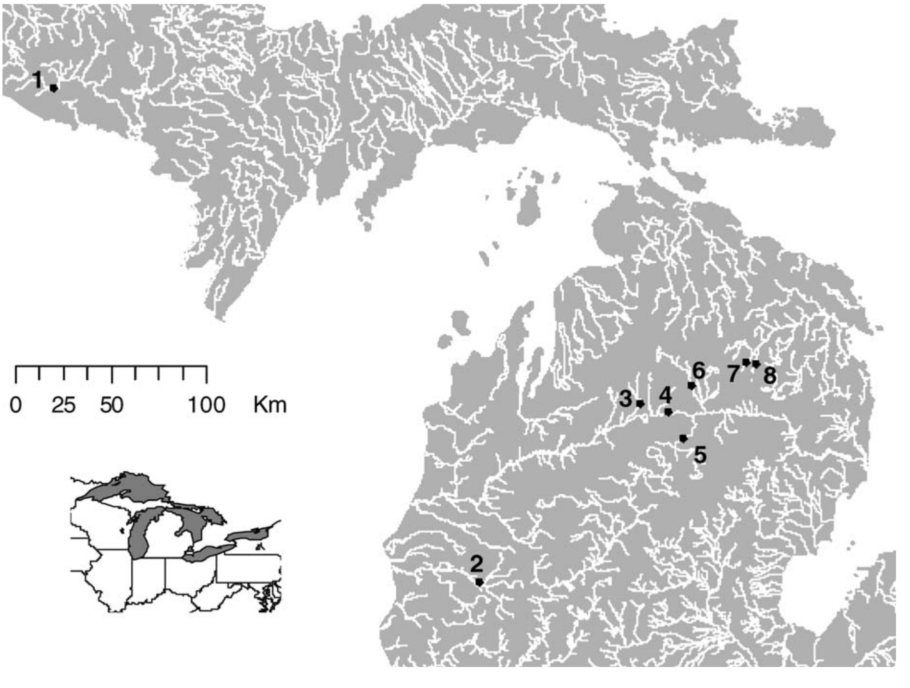

FIGURE 1.—Map of northern Michigan showing the rivers with long-term fish population data used in this study. Rivers are as follows: (1) South Branch Paint, (2) Pere Marquette, (3) Manistee, (4) main-stem Au Sable, (5) South Branch Au Sable, (6) North Branch Au Sable, (7) Hunt Creek, and (8) Gilchrist Creek.

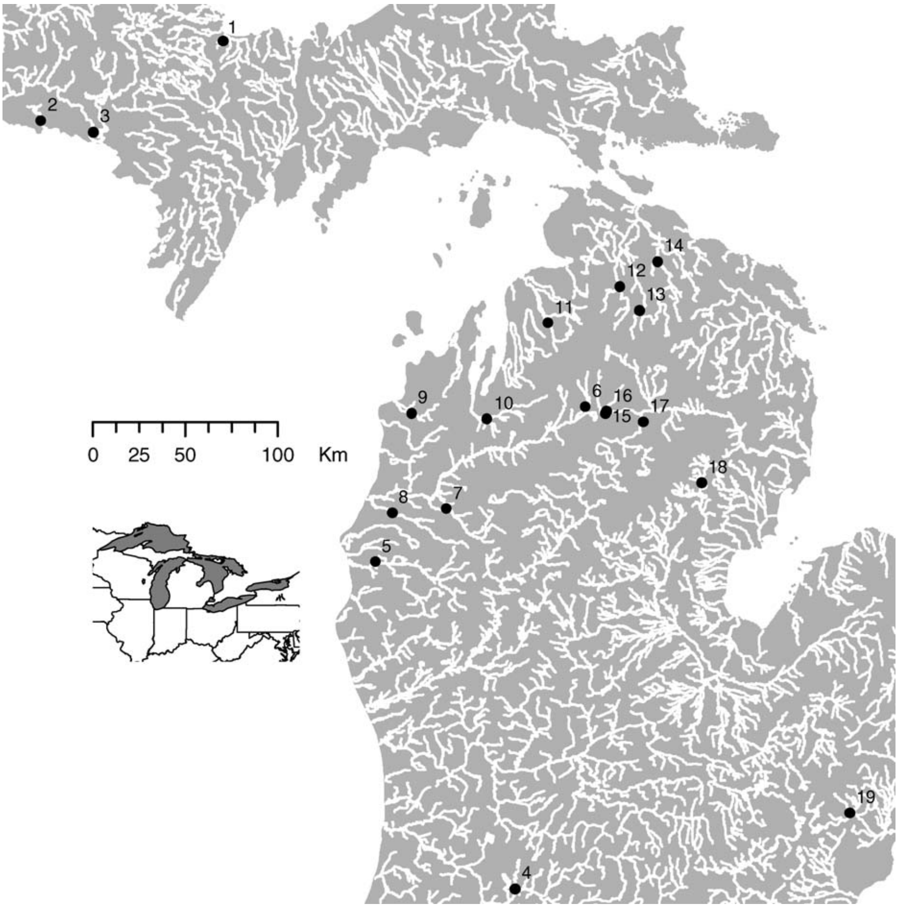

FIGURE 2.—Map showing the locations of the U.S. Geological Survey streamflow gauges from which data were obtained for this study. Additional information on these locations is presented in Table 2.

peak spawning times for brown trout (i.e., when most egg fertilization presumably occurred) were identified from weekly redd counts conducted in Hunt Creek during 1997–2001 and in the main-stem and South Branch Au Sable River for 1999–2000 and provided starting dates for model runs. Water temperatures were measured hourly in the four streams with electronic thermometers. We predicted the number of days to 50% swim-up of brown trout fry (assuming peak spawning happens at the same time each year) for years with daily water temperature measurements during the incubation period. We compared 50% swim-up dates (i.e., the number of days after 1 January) for brown trout fry among rivers using analysis of variance (ANOVA) techniques with river and year as random effects. We used the Bonferroni test for multiple comparisons among rivers and a significance level of 0.05. Data analyses were done with SPSS version 11.5 (SPSS 2002).

Results

Synchrony of Year-Class Densities and Spring Flows among Rivers

The occurrence of synchrony in brown trout and brook trout reproductive success among rivers was supported by significant correlations in age-class density (Tables 3, 4). Significant positive correlations in age-0 brown trout density occurred among sites on rivers draining into Lake Michigan (Manistee River, Pere Marquette River) and Lake Huron (Au Sable River system, Gilchrist Creek). Positive correlations in densities of older age-classes among rivers were also apparent, suggesting general synchrony among streams in regards to strong or weak year-classes through time (Table 3). For example, we observed significant correlations among sites in densities of age-1 and age-2 brown between the main-stem Au Sable River and other rivers including the North and South branches of the Au Sable River, Gilchrist Creek, Hunt

TABLE 3.—Correlations in year-class density for age-0, age-1, and age-2 brown trout from various Michigan rivers with sample sizes in parentheses. Positive correlations significant at $P \leq 0.10$ are denoted by asterisks. Sites used on the Au Sable River were Smith Bridge (South Branch), Eamon's Landing (North Branch), and Thendara Road (main stem).

Stream	South Branch Au Sable River	North Branch Au Sable River	Main-stem Au Sable River	Manistee River	Pere Marquette River	Gilchrist Creek	South Branch Paint River
Age-0							
North Branch Au Sable River	0.69* (22)						
Main-stem Au Sable River	0.21 (23)	0.60* (27)					
Manistee River	0.62* (16)	0.69* (12)	0.59* (14)				
Pere Marquette River	0.64* (19)	0.84* (16)	0.31 (16)	0.65* (15)			
Gilchrist Creek	0.51 (9)	0.57 (6)	0.12 (7)	0.39 (9)	0.73* (9)		
South Branch Paint River	0.04 (14)	−0.05 (10)	0.19 (12)	0.03 (14)	−0.22 (13)	−0.70 (10)	
Hunt Creek	0.11 (9)	−0.20 (6)	0.07 (7)	0.37 (9)	0.38 (9)	−0.13 (9)	0.29 (9)
Age-1							
North Branch Au Sable River	0.47* (22)						
Main-stem Au Sable River	0.36* (23)	0.72* (27)					
Manistee River	−0.02 (16)	0.25 (12)	−0.42 (14)				
Pere Marquette River	−0.01 (19)	−0.30 (16)	−0.14 (16)	−0.41 (15)			
Gilchrist Creek	0.31 (9)	0.04 (6)	0.87* (7)	−0.33 (9)	0.16 (9)		
South Branch Paint River	0.49* (14)	0.77* (10)	0.18 (12)	−0.03 (14)	−0.19 (13)	0.22 (10)	
Hunt Creek	0.09 (9)	−0.07 (6)	0.85* (7)	−0.61 (9)	0.33 (9)	0.61 (9)	−0.10 (9)
Age-2							
North Branch Au Sable River	0.62* (22)						
Main-stem Au Sable River	0.71* (23)	0.73* (27)					
Manistee River	0.21 (16)	−0.05 (12)	−0.07 (14)				
Pere Marquette River	0.27 (19)	0.43 (16)	0.70* (16)	0.18 (15)			
Gilchrist Creek	0.50 (9)	0.01 (6)	0.42 (7)	0.32 (9)	0.35 (9)		
South Branch Paint River	0.00 (14)	0.61* (10)	0.04 (12)	0.40 (14)	0.06 (13)	0.17 (10)	
Hunt Creek	−0.40 (9)	−0.31 (6)	0.63 (7)	−0.27 (9)	0.10 (9)	0.30 (9)	0.06 (9)

Creek, and the Pere Marquette River. Correlated sites were often widely separated, as was the case for the Au Sable and Pere Marquette rivers, which drain into different Great Lakes and were surveyed at sites approximately 140 km apart (Figure 3).

Correlations in age-class density of brook trout among rivers also supported the hypothesis of regional synchrony, though data were available from fewer streams. Age-0 densities of brook trout were significantly correlated among the three Au Sable River branches, as well as between the Manistee River and Hunt Creek (Table 4). Synchrony among sites was also apparent from significant correlations in age-1 brook trout densities among sites (Table 4). Synchrony in age-class density even seemed evident between some streams, such as the Manistee River and Hunt Creek, where correlation coefficients were not statistically significant (Figure 4). Densities of various age-classes of both brown trout and brook trout were also highly correlated between sites within each branch of the Au Sable River (T. Zorn and A. Nuhfer, unpublished data).

We identified several regional groupings of rivers based on correlations in average May discharge (Table 5; Figure 5). The most notable group, the north-central Lower Peninsula (LP) rivers, flows off of deep glacial outwash deposits and includes the

TABLE 4.—Correlations in year-class density for age-0 and age-1 brook trout from various Michigan rivers with sample sizes in parentheses. See Table 3 for additional details.

Stream	South Branch Au Sable River	North Branch Au Sable River	Main-stem Au Sable River	Manistee River
Age-0				
North Branch Au Sable River	0.24 (22)			
Main-stem Au Sable River	0.48* (23)	0.37* (27)		
Manistee River	−0.37 (16)	−0.08 (12)	−0.13 (14)	
Hunt Creek	0.28 (7)	−0.85* (5)	0.14 (6)	0.80* (7)
Age-1				
North Branch Au Sable River	−0.06 (22)			
Main-stem Au Sable River	0.49* (23)	0.24 (27)		
Manistee River	−0.11 (16)	0.46 (16)	0.56* (14)	
Hunt Creek	−0.58 (7)	−0.80 (5)	0.91* (6)	0.55 (7)

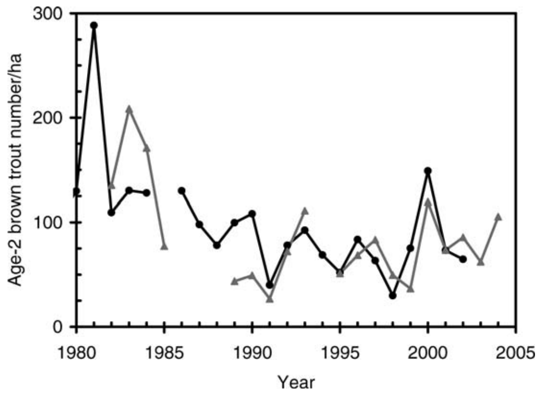

FIGURE 3.—Age-2 brown trout density over time at sites 140 km apart on two Michigan rivers, the main-stem Au Sable (black circles) and Pere Marquette (gray triangles).

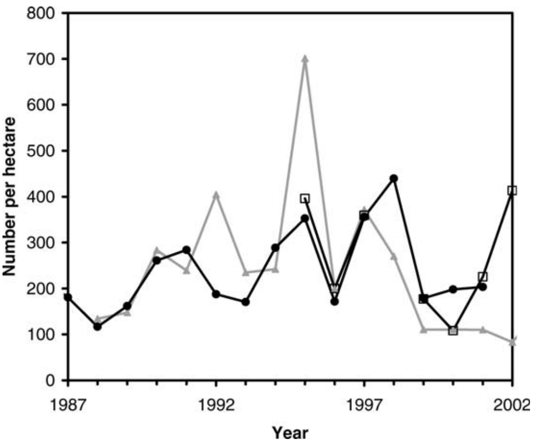

FIGURE 4.—Age-1 brook trout density (number/ha) over time in the Manistee River (gray triangles), main-stem Au Sable River (black circles), and Hunt Creek (open squares).

following rivers (gauge sites): Manistee, Boardman, Platte, Jordan, Sturgeon, Pigeon, Black, and main-stem, South Branch, and East Branch Au Sable (Figure 2; Figure 5). These rivers represent many of Michigan's important trout streams. Another group of rivers (Pere Marquette, Pine, and Little Manistee) are most similar to each other, but also share spring flow characteristics with the previous group (Figure 2, 5). These rivers all drain coarse-textured moraines and glacial outwash in the northwestern LP. Spring flows in the Rifle River are correlated fairly well with those of the South Branch Au Sable River, though not as well with other north-central LP rivers (Table 5). Paint and Augusta creeks, southern streams on opposite sites of the LP, had spring flows most similar to each other and somewhat similar to trout streams farther north (Table 5; Figure 5). Spring flows of two trout streams in the western Upper Peninsula (UP; South Branch Paint and Iron rivers) were highly correlated, though neither was correlated hydrologically with Cherry Creek, whose watershed has a colder climate due to its location along the south shore of Lake Superior (Table 5; Figure 5).

Swim-Up Dates of Fry in Rivers

Before predicting mean swim-up times of brown trout in rivers, we evaluated models developed to predict times of 50% hatch and swim-up of brown trout fry (Crisp 1981, 1988) to determine whether they would yield accurate predictions given the cold winter temperatures of Michigan streams. Winter temperatures in Michigan rivers are several degrees colder than those used in development of Crisp's (1981, 1988) models, but his predictions proved to be reasonably accurate based upon data we collected when rearing brown trout at near-ambient winter temperatures in a hatchery. Correlations between predicted and observed numbers of days from fertilization to 50% hatch and swim-up of brown trout fry under these conditions were 0.77 and 0.98, respectively (Zorn and Nuhfer, unpublished data), suggesting the model for predicting 50% swim-up (Crisp 1988) would be valid for Michigan trout streams.

For 1996–2005, the average 50% swim-up dates ranged from 21 April in Gilchrist Creek to 1 May in the South Branch Au Sable River (Table 6). River had a significant effect ($F = 23.8$; df $= 3, 33$; $P < 0.001$) with 50% swim-up in Hunt and Gilchrist creeks occurring roughly 1 week earlier than in the main-stem and South Branch Au Sable rivers (Table 6). Estimated date of 50% swim-up varied synchronously among rivers with winter severity ($F = 25.8$; df $= 14, 32$; $P < 0.001$), being as late as May 18 after very cold winters (Figure 6). The river $\times$ year interaction term was not significant.

Discussion

Regional Influences on Population Dynamics

Our analyses provide several compelling lines of support for the hypothesis that the population dynamics of brown trout and brook trout in Michigan's low-gradient streams are driven largely by processes operating at the regional scale. Analysis of several decades of brown trout and brook trout density data for the Au Sable River demonstrated the importance of year-class strength (reproductive success) in determining densities of the same cohort at older ages (Zorn and Nuhfer 2007, this issue). Variation in age-0 year-class density was difficult to explain in their study but was positively associated with spawner (or egg) density

TABLE 5.—Pearson correlations in average May discharge among Michigan trout streams and number of years (parentheses) for which comparisons could be made. All correlations with asterisks are significant at $P \leq 0.05$; those in bold italics have correlation coefficient values ≥ 0.7 while those in bold alone have correlation coefficients ≥ 0.5 and < 0.7.

Stream	Iron River	Paint River	Augusta Creek	Pere Marquette River	Manistee River	Pine River	Little Manistee River	Platte River	Boardman River
Cherry Creek	−0.02 (6)	0.28 (7)	0.45 (7)	−0.36 (7)	0.24 (5)	0.22 (7)	−0.31 (5)	(0)	−0.43 (7)
Iron River		***0.89**** (28)	0.18 (16)	0.33 (33)	0.37 (26)	0.34 (28)	0.37 (19)	(0)	0.28 (28)
Paint River			0.11 (40)	0.07 (52)	0.46* (21)	0.17 (30)	0.22 (19)	0.06 (15)	0.18 (37)
Augusta Creek				**0.56*** (40)	−0.08 (9)	0.44 (18)	−0.05 (11)	0.46 (15)	0.36 (25)
Pere Marquette River					**0.66*** (31)	***0.91**** (30)	***0.87**** (19)	0.49 (15)	**0.61*** (37)
Manistee River						**0.63*** (21)	***0.80**** (17)	(0)	***0.80**** (21)
Pine River							***0.88**** (19)	(0)	***0.72**** (30)
Little Manistee River								(0)	***0.79**** (19)
Platte River									(0)
Boardman River									
Jordan River									
Sturgeon River									
Pigeon River									
Black River									
Main-stem Au Sable River									
East Branch Au Sable River									
South Branch Au Sable River									
Rifle River									

from the previous fall and negatively influenced by high flow conditions at or near the time of fry emergence in spring. Thus, initial reproductive success appears to be a key factor influencing overall population dynamics of trout in Michigan streams. Still, densities at sites may be significantly influenced by local habitat factors, including nutrient levels, water temperature, and large woody debris (Zorn and Nuhfer 2007).

Our regional streamflow analysis found considerable year-to-year synchrony in flow conditions among streams at the time of trout fry emergence (Table 5; Figure 5). Despite consistent differences in 50% fry emergence dates among rivers, winter climate conditions influence river temperatures (and incubation time of eggs and fry) similarly among streams in regions of the state and contribute to interannual synchrony among rivers in emergence times of trout fry (Figure 6). These processes collectively favor the synchrony in year-class strength and densities of older age-classes observed among our study streams due to strong carryover of age-classes (Zorn and Nuhfer 2007). Such carryover of strong or weak year-classes can eventually influence future spawning stock size and egg deposition. Lobón-Cerviá (2005) reported that over 90% of the variation in lifetime density of brown trout cohorts at four sites on a Spanish river was explained by variation in recruitment.

Hydrologic influences on brown trout year-class strength have been observed previously in Michigan (Nuhfer et al. 1994) as well as in other states and European countries (e.g., Strange et al. 1992; Cattanéo et al. 2002, 2003; Lobón-Cerviá 2004; Lobón-Cerviá and Rincón 2004). Nehring and Anderson (1993) found that variable recruitment of age-0 brown trout and rainbow trout *Oncorhynchus mykiss* in 10 Colorado streams over a 13-year period was largely attributable to variation in mean monthly discharge

TABLE 5.—Extended.

Stream	Jordan River	Sturgeon River	Pigeon River	Black River	Main-stem Au Sable River	East Branch Au Sable River	South Branch Au Sable River	Rifle River	Paint Creek
Cherry Creek	0.25	−0.14	−0.25	0.02	−0.09	−0.09	−0.30	0.35	0.56
	(6)	(7)	(7)	(7)	(7)	(7)	(6)	(7)	(7)
Iron River	0.30	**0.55***	**0.56***	**0.51***	0.44	**0.51***	0.27	0.23	−0.06
	(14)	(33)	(30)	(33)	(33)	(23)	(14)	(30)	(21)
Paint River	0.24	0.39*	0.36*	0.40*	0.42*	0.49*	0.19	0.09	0.09
	(38)	(52)	(52)	(48)	(41)	(27)	(37)	(30)	(45)
Augusta Creek	0.43*	0.41*	0.44*	0.44*	**0.50***	0.41	**0.55***	0.27	**0.68***
	(38)	(40)	(40)	(36)	(29)	(20)	(37)	(18)	(40)
Pere Marquette River	**0.51***	0.48*	0.41*	**0.50***	**0.61***	**0.63***	**0.67***	0.38*	**0.65***
	(38)	(63)	(54)	(58)	(51)	(27)	(37)	(32)	(45)
Manistee River	***0.97****	***0.78****	0.62*	***0.80****	***0.93****	***0.97****	**0.67***	0.43*	0.06
	(7)	(31)	(23)	(31)	(31)	(16)	(7)	(23)	(14)
Pine River	**0.65***	**0.57***	**0.57***	**0.54***	***0.71****	***0.70****	**0.65***	0.29	**0.53***
	(16)	(30)	(30)	(30)	(30)	(25)	(16)	(30)	(23)
Little Manistee River	0.26	**0.57***	**0.52***	**0.55***	***0.71****	**0.66***	**0.57***	0.47*	0.18
	(9)	(19)	(19)	(19)	(19)	(18)	(9)	(19)	(16)
Platte River	***0.74****	***0.82****	***0.78****	***0.78****	0.75		***0.73****		0.26
	(15)	(15)	(15)	(11)	(4)	(0)	(14)	(0)	(15)
Boardman River	***0.70****	***0.76****	***0.75****	***0.75****	***0.85****	***0.83****	***0.72****	0.36*	0.32
	(23)	(37)	(37)	(37)	(37)	(27)	(23)	(30)	(30)
Jordan River		***0.81****	***0.84****	***0.89****	***0.77****	***0.83****	**0.64***	0.31	0.41*
		(38)	(38)	(34)	(27)	(18)	(37)	(16)	(38)
Sturgeon River			***0.91****	***0.88****	***0.79****	***0.92****	***0.73****	0.34	0.30*
			(54)	(58)	(51)	(27)	(37)	(32)	(45)
Pigeon River				***0.92****	***0.75****	***0.85****	***0.70****	0.48*	0.32*
				(50)	(43)	(27)	(37)	(32)	(45)
Black River					***0.76****	***0.91****	***0.74****	0.49*	0.29
					(51)	(27)	(33)	(32)	(41)
Main-stem Au Sable River						***0.96****	**0.69***	0.38*	0.39*
						(27)	(26)	(32)	(34)
East Branch Au Sable River							***0.74****	0.41*	0.32
							(18)	(25)	(25)
South Branch Au Sable River								**0.62***	**0.66***
								(16)	(37)
Rifle River									0.34
									(23)

during the fry life stage. Spina (2001) observed an inverse relationship between peak discharge during incubation and density of age-0 brown trout in a high-gradient California stream, along with carryover of relative year-class strength to older age-groups. However, all of the aforementioned studies except Nuhfer et al. (1994) occurred in high-gradient mountainous streams. Our findings suggest that these processes operate in hydrologically stable, low-gradient streams, although the strength of the effect seems somewhat reduced (Zorn and Nuhfer 2007).

Redd scour is often postulated as the cause of reduced reproductive success of brown trout (Anderson 1983; Spina 2001) and brook trout (Seegrist and Gard 1972; Hanson and Waters 1974; Erman et al. 1988; Carline and McCullough 2003). We have no data to determine if redd scour is a plausible explanation for lower reproductive success in our study streams. However, spring observations of gravel riffles in the Au Sable River system and in Hunt and Gilchrist creeks revealed only localized areas of gravel scour. In addition, the highest daily spring discharge during our study period on the South Branch Au Sable River (1974–2003) occurred on March 29, 1976, yet the 1976 year-class of brown trout was only 10% lower than the long-term average. Most age-0 trout would have been in redds at that time so significant scouring of redds was unlikely.

The displacement and mortality of recently emerged fry seems a key factor limiting the reproductive success of trout in our study streams. Water velocities sufficient to displace brown trout alevins and fry (Ottaway and Forrest 1983) are common in unprotected microhabitats in Michigan streams during spring floods. Lobón-Cerviá (2004) emphasized the importance of discharge conditions during or just after brown trout emergence as the main determinant of recruitment in a river in northwestern Spain.

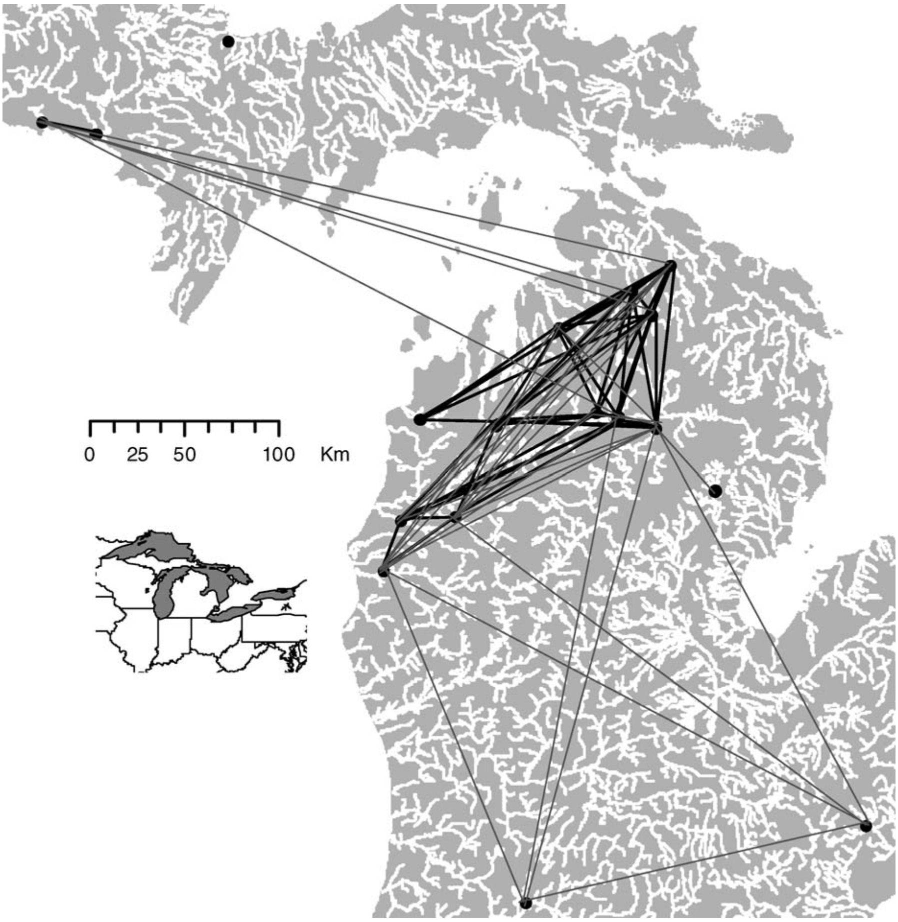

FIGURE 5.—Lines showing the correlations in average May discharge between selected U.S. Geological Survey sites on Michigan rivers. All correlations were significant at the 0.05 level. Black lines indicate correlations with Pearson $r \geq 0.7$, gray lines those with $r \geq 0.5$ and <0.7; significant correlations with $r < 0.5$ are not shown.

The estimated time when most brown trout fry were predicted to emerge from redds was usually after peak spring runoff. For example, in the South Branch Au Sable River peak spring runoff usually occurred during the second week of April, roughly 10 d earlier than the predicted mean emergence date for the 1996–2005 year-classes. Progeny of brown trout that spawned earlier than the dates used in our model, or those that spawned in areas of groundwater upwelling, would likely emerge closer to peak spring runoff periods.

TABLE 6.—Estimated earliest, average, and latest swim-up dates for brown trout fry in four Michigan streams during 1996–2005. Mean swim-up dates were projected using the dates of peak spawning, daily incubation temperatures, and the equations in Crisp (1981, 1988). Redd count observations indicated that peak spawning generally occurred on 25 October in Hunt and Gilchrist creeks, 7 November in the South Branch Au Sable River, and 15 November in the main-stem Au Sable River.

Stream	Earliest	Average	Latest
Hunt Creek	10 Apr	23 Apr	14 May
Gilchrist Creek	12 Apr	21 Apr	8 May
Main-stem Au Sable River	18 Apr	29 Apr	17 May
South Branch Au Sable River	12 Apr	1 May	18 May

We are unaware of other studies demonstrating the effects of flow conditions during fry emergence on brook trout reproductive success, and our regression analyses for brook trout in the Au Sable River did not identify such flows as predictors of age-0 density (Zorn and Nuhfer 2007). However, synchrony in densities of brook trout age-groups among hydrologically stable Michigan rivers (Table 4) suggests that regional climatic conditions and their effects on stream hydrology similarly influence brook trout reproductive success in a given year and population dynamics.

By correlating flow conditions and year-class

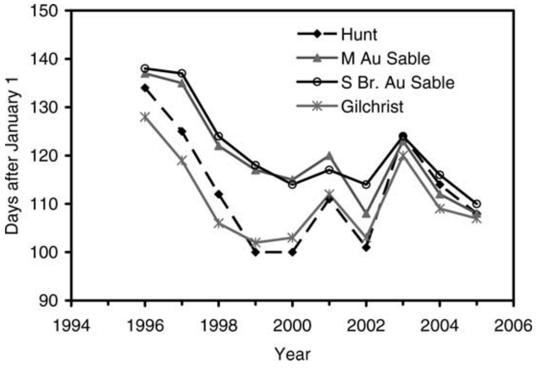

FIGURE 6.—Estimated mean swim-up dates for brown trout fry (expressed as the number of days after 1 January) in four Michigan streams during 1996–2005. Values were projected using the dates of peak spawning, daily incubation temperatures, and the equation in Crisp (1988). Redd count observations indicated that peak spawning generally occurred on 25 October in Hunt and Gilchrist creeks, 7 November in the South Branch Au Sable River, and 15 November in the main-stem Au Sable River.

density among several rivers, our study begins to describe the spatial scale at which synchrony in stream hydrology and trout reproductive success may occur. Strong correlations in age-class densities among Michigan rivers demonstrate the importance of regional processes to population dynamics of Midwestern stream fishes. Extensive correlations in May discharge among many trout streams in the north-central and northwest Lower Peninsula of Michigan (Figure 5) suggest that trout population dynamics may be synchronous for many streams in this region. Distances between sites with significant correlations in trout year-class density (up to 140 km) in our study were greater than those noted previously. Lobón-Cerviá (2004) observed synchrony in brown trout recruitment among Spanish stream sites less than 30 km apart and concluded that similarities in streamflow levels among sites during or just after emergence was responsible for the synchrony observed in brown trout population dynamics. Myers et al. (1997) hypothesized a 50-km spatial scale within which recruitment synchrony would be expected for freshwater fish. Gowan and Fausch (1996) observed synchronous changes in adult trout abundance within six Colorado streams and among streams up to 60 km apart.

There are several possible reasons why correlation values and their significance differed among streams and age-classes. Effects of spates on reproductive success may vary among sites due to physical characteristics of sites that buffer them from the effects of high flows. Characteristics may include low stream gradients or woody or off-channel habitats that provide a refuge from high current velocities. Physical characteristics of sites may also influence fish abundance and age structure of the catch at index stations through source-sink processes (i.e., density-dependent immigration and emigration), which in turn may limit spatial correlations in age-class density. Relatively short population sampling reaches (compared with the larger home range of older trout) may have limited the accuracy of density estimates and our ability to detect correlations among older age-classes. We did not attempt to correlate abundances of age-3 and older brown trout and age-2 and older brook trout for this reason. Local-scale variation in climate or human influences on rivers in a region can also lead to slightly different recruitment patterns among streams. For example, lake-level management upstream of the South Branch Au Sable River site was suspected to influence the river's spring flow conditions and brown trout recruitment in some years (Nuhfer et al. 1994).

The life history and reproductive behavior of resident brown trout in Michigan rivers seems conducive to year-to-year synchrony in recruitment among streams. Our limited predictions of emergence times and data on spring flow conditions suggest that brown trout emergence often occurs shortly after peak spring flows. Timing of emergence to avoid peak runoff may optimize the trade-off between avoiding mortality due to peak flows (i.e., increasing reproductive success) and maximizing opportunity for growth and survival of fry by earlier emergence during years with more stable spring flows. Similarity of predicted swim-up dates among streams where we had data on spawning activity supports the notion that brown trout fry may be equally vulnerable to spring flow conditions among rivers over broad geographic areas with similar climates. As a result, reproductive success and general population dynamics may be synchronous among such rivers.

Extensive correlations among spring flow conditions across Michigan and synchrony in swim-up times among rivers (Figures 5, 6) set the stage for future regional-scale studies of trout population dynamics (Cattanéo et al. 2003). Limited long-term population trend data we have for trout suggest the occurrence of such regional-scale trends in portions of Michigan. A network of trout population-monitoring stations established as part of the Michigan Department of Natural Resources (MDNR) Fisheries Division's Stream Status and Trends Program will greatly aid in further study of the spatial extent of synchrony in fish population dynamics throughout Michigan. The network consists of roughly 70 trout and smallmouth bass *Micropterus dolomieu* population index sites, located near USGS gauges when possible, that will provide long-term trend data on fish population dynamics. These data will enhance our ability to define regions of Michigan where stream fish populations vary in synchrony. With knowledge of regional trends in trout populations providing context for interpreting data from individual surveys, managers will be better able to assess survey findings, evaluate management practices, and determine the need for further management action.

Limitations of the Analysis

The robustness of the findings of our analyses are somewhat limited by the data available as well as our selection of regional-scale variables to study. Trout population estimates were made in relatively short (<400-m) reaches and may not have always provided an accurate index of actual population density in longer reaches. Our analysis of correlations among flows on trout streams was limited to locations of USGS streamflow gauges, some of which occurred on warmer downstream reaches of trout streams. In all but a few cases (e.g., South Branch Paint River) the gauge and trout-inhabited reaches were probably in close enough proximity that this was not a problem. Nevertheless, having flow gauges in the reaches where fish surveys occurred would have helped in assessing regional similarities in spring discharge among rivers and their effects on trout reproduction.

We did not explore the regional-scale effects of other aspects of climate on trout year-class strength but suspect that they also contribute to synchrony. For example, negative associations between winter air temperatures and age-class density and between summer stream temperatures and trout growth that we found for some age-group s of trout in the Au Sable River (Zorn and Nuhfer 2007) reflect local responses to regional climate conditions. Such responses may be expected in hydrologically similar streams across a region and would likely further contribute to synchrony in fish population dynamics.

We think the primary cause of the negative effect of flow on age-0 trout density relates to the increased velocity that occurs at high flows. Relations among velocity, streamflow, and age-0 trout density might be influenced by site-scale factors such as stream gradient or cover, but such local-scale data were not available in our study. Further research into the relationships among stream discharge, current velocity, gradient, and site-scale aspects of habitat complexity and their influences on emerging trout fry would be beneficial.

Management Implications

Given limited resources, fishery managers are tasked with making the most efficient use of available resources and extracting the maximum amount of information from the data collected. Using well-targeted survey effort to understand and describe temporal trends in stream trout populations across a region would be a powerful tool for fishery managers. With such knowledge as a benchmark, managers can better interpret findings of individual surveys within a region and be more informed when deciding on the need for further management action. By using a network of fixed trout population index sites in its Streams Status and Trends Program, the MDNR Fisheries Division is working to identify synchronous populations of stream trout and the appropriate spatial scales for describing trends in stream trout populations. Knowledge of where trout populations fluctuate in synchrony would greatly aid in reporting on the status of naturally reproducing trout stocks throughout the state to the public.

Knowledge of which populations are in synchrony also opens up opportunities to use long-term population index data to address issues in other rivers where trend data are limited. For example, a long-standing controversy exists as to whether the resident brown trout population of the Pere Marquette River declined due to introduction of Pacific salmonids or to other causes. Correlations in trout population trends between the main-stem Au Sable and the Pere Marquette rivers (Table 3; Figure 3) suggest that brown trout trends in the Au Sable River could be used to predict trout densities in the Pere Marquette River for years when there was no survey data. Data on main-stem Au Sable River brown trout suggests that the brown trout population in the Pere Marquette River may have declined on its own during the 1970s and 1980s, with changes beyond those predicted from the Au Sable River potentially related to other factors such as presence of Pacific salmonids. Other applications of these long-term index data will certainly emerge as our knowledge of the spatial extent of synchronous trout populations improves.

Acknowledgments

This study would not have been possible without the contributions of many. Michigan Department of Natural Resources Fisheries Division field crews based from Grayling, Gaylord, Cadillac, and Crystal Falls conducted fish population surveys, with assistance from other MDNR offices and volunteers throughout the state. Streamflow data were provided by the USGS and S. Aichele provided the data layer for mapping USGS streamflow gauges. Redd count reaches were established on the Au Sable River under guidance of G. Alexander. Field assistance with redd counts and temperature data collection was provided by T. Adams and T. Smigielski. Helpful comments on this manuscript and analytic insights were provided by P. Schneeberger, D. Hayes, and T. Wills. Financial support for this study came from the Federal Aid in Sport Fish Restoration Fund (F-80-R) and the MDNR Fish and Game fund.

References

Anderson, D. W. 1983. Factors affecting brown trout reproduction in southeastern Minnesota streams. Minnesota Department of Natural Resources, Investigational Report 376, St. Paul.

Carline, R. F., and B. J. McCullough. 2003. Effects of floods on brook trout populations in the Monongahela National Forest, West Virginia. Transactions of the American Fisheries Society 132:1014–1020.

Cattanéo, F., B. Hugueny, and N. Lamouroux. 2003. Synchrony in brown trout, *Salmo trutta*, population dynamics: a 'Moran effect' on early life stages. Oikos 100:43–54.

Cattanéo, F., N. Lamouroux, P. Breil, and H. Capra. 2002. The influence of hydrological and biotic processes on brown trout (*Salmo trutta*) population dynamics. Canadian Journal of Fisheries and Aquatic Sciences 59:12–22.

Crisp, D. T. 1981. A desk study of the relationship between temperature and hatching time for the eggs of five species of salmonid fishes. Freshwater Biology 11:361–368.

Crisp, D. T. 1988. Prediction, from temperature, of eyeing, hatching, and 'swim-up' times for salmonid embryos. Freshwater Biology 19:41–48.

Erman, D. C., E. D. Andrews, and M. Yoder-Williams. 1988. Effects of winter floods on fishes in the Sierra Nevada. Canadian Journal of Fisheries and Aquatic Sciences 45:2195–2200.

Gowan, C., and K. D. Fausch. 1996. Long-term demographic responses of trout populations to habitat manipulation in six Colorado streams. Ecological Applications 6:931–946.

Hanson, D. L., and T. F. Waters. 1974. Recovery of standing crop and production rate of a brook trout population in a flood-damaged stream. Transactions of the American Fisheries Society 103:431–439.

Jensen, A. J., and B. O. Johnsen. 1999. The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). Functional Ecology 13:778–785.

Lobón-Cerviá, J. 2004. Discharge-dependent covariation patterns in the population dynamics of brown trout (*Salmo trutta*) within a Cantabrian river drainage. Canadian Journal of Fisheries and Aquatic Sciences 61:1929–1939.

Lobón-Cerviá, J. 2005. The importance of recruitment for the production dynamics of stream-dwelling brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 62:2484–2493.

Lobón-Cerviá, J., and P. A. Rincón. 2004. Environmental determinants of recruitment and their influence on the population dynamics of stream-dwelling brown trout *Salmo trutta*. Oikos 105:641–646.

Myers, R. A., G. Mertz, and J. Bridson. 1997. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. Canadian Journal of Fisheries and Aquatic Sciences 54:1400–1407.

Nehring, R. B., and R. M. Anderson. 1993. Determination of population-limiting critical salmonid habitats in Colorado streams using the Physical Habitat Simulation System. Rivers 4:1–19.

Nuhfer, A. J., R. D. Clark, Jr., and G. R. Alexander. 1994. Recruitment of brown trout in the South Branch of the Au Sable River, Michigan, in relation to stream flow and winter severity. Michigan Department of Natural Resources, Fisheries Research Report 2006, Ann Arbor.

Ottaway, E. M., and D. R. Forrest. 1983. The influence of water velocity on the downstream movement of alevins and fry of brown trout, *Salmo trutta* L. Journal of Fish Biology 23:221–227.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Seegrist, D. W., and R. Gard. 1972. Effects of floods on trout in Sagehen Creek, California. Transactions of the American Fisheries Society 101:478–482.

Spina, A. P. 2001. Incubation discharge and aspects of brown trout population dynamics. Transactions of the American Fisheries Society 130:322–327.

SPSS. 2002. SPSS base user's guide 11.5. SPSS, Chicago.

Strange, E. M., P. B. Moyle, and T. C. Foin. 1992. Interactions between stochastic and deterministic processes in stream fish community assembly. Environmental Biology of Fishes 36:1–15.

Wiley, M. J., S. L. Kohler, and P. W. Seelbach. 1997. Reconciling landscape and local views of aquatic communities: lessons from Michigan trout streams. Freshwater Biology 37:133–148.

Zorn, T. G., and A.J. Nuhfer. Influences on brown trout and brook trout population dynamics in a Michigan river. Transactions of the American Fisheries Society 136:691–705.